

TERRITORIALITY AND DISPERSAL IN DRAGONFLIES (ODONATA)¹

BY EDWARD J. KORMONDY

DEPARTMENT OF ZOOLOGY, OBERLIN COLLEGE, OBERLIN, OHIO

Investigation of territoriality occurred first in birds and led eventually to Howard's (1920) clarifying exposition, Heape's (1931) extension of the concept to other animals, and ultimately to the widely accepted precept that it is a behavioral phenomenon characterized by an organism maintaining a "defended area" (Nobel, 1939; Nice, 1941). Carpenter (1958) has reviewed territorial behavior in vertebrates; there is no comparable review for invertebrates. Carthy's (1958) study on invertebrate behavior contains no reference to territoriality; Thorpe (1956) has only a cursory statement about the phenomenon in higher crustacea and a few insects. Aside from the several papers on Odonata to be discussed presently, territorial behavior in invertebrates has been postulated on sound evidence for only a few forms such as the fiddler crab *Uca* (Verwey, 1930 and Crane, 1941), the burrowing beetles of the genus *Necrophorus* (Pukowski, 1933) and the ants *Formica rufa* (Elton, 1932), and *Formica fusca*, *Acanthomyops niger* and *Myrmica scabrinodis* (Pickles, 1935). The lack of attention to territoriality among invertebrates may be occasioned by infrequent occurrence; however, it *may* also be the case that it is not being recognized because of a too rigid concept of what constitutes this type of behavior.

If in the more intensively studied vertebrates it can still be stated that in the investigation of territoriality, information is largely limited and qualitative, and formulation and testing of hypotheses is merely beginning (Carpenter, 1958), one can underscore the same limitations as regards invertebrates. While there is need for compilation on this level, the present paper is restricted to a review of territorial behavior only in dragonflies—its occurrence, characteristics, significance and possible relationships with dispersal.

¹ Read as part of a symposium on "Mechanisms of Species Dispersal" held by the Systematics and General Entomology Section, Entomological Society of America, North Central Branch, March 25, 1959, Columbus, Ohio.

TERRITORIALITY

During a study of the systematics of the species of *Tetragoneuria* occurring in the Great Lakes region (Kormondy, 1959), territorial behavior was observed in several species, notably *Tetragoneuria cynosura* (Say). Marking studies, largely inconclusive, were combined with observation to investigate a number of behavioral characteristics, among them territoriality. In this activity, males on a lake shore are spaced in intervals varying directly with the population density, the latter in turn varying both seasonally and diurnally. At the time of greatest seasonal density males flew in intervals of 10 to 30 feet, 1 to 3 feet from shore and 3 feet above the water; these spaces coincided closely with microtopographic areas delimited by overhanging shrubs if the latter occurred in the habitat. There is a tendency for the male to become localized in these microtopographic areas, or at least in given sectors of the area. This localization tendency was tested artificially by swishing a net near the male, who either shifted to a spot some 10 to 20 feet away, or flew upward some 30 feet and returned to the same position. Localization is observed also in response to incursions by similar-sized dragonflies which resulted in an exploratory response of quick flight and were almost invariably followed by a return to the original area. The flight pattern of the male at this time is characterized by extended periods of hovering (up to 15 minutes or longer), considerable maneuvering and no alighting. By contrast, feeding flight occurs away from the water, and is characterized by little or no hovering, both vertical and considerable horizontal displacement, and a height of usually 6 feet above ground. No spacing, although some tendency to localize, occurs in feeding behavior.

When the *Tetragoneuria cynosura* male is in his territory and is approached by another *cynosura* of either sex, the exploratory response, a quick flight simulating a chase, gives way to aggressive behavior. Visual perception of another *cynosura* appears to be the mechanism releasing aggressive behavior. This aggressive behavior appears to be sexually motivated since there is an attempt by the occupant male to achieve the precopulatory tandem position with the intruder regardless of its sex. If the intruder is a male, agonistic reactions displace sexual ones, and

a clash or "fight" occurs; if the intruder is a female, copulatory activity ensues. The stimuli allowing the perception of sex upon contact are unstudied.

With this resumé of behavior in *Tetragoneuria* as background and before turning to additional cases in Odonata it would be well to review briefly the concept of territorial behavior. Carpenter (1958) has noted that the many definitions of territoriality which have been advanced are based largely on bird behavior and do not represent the complete range of variability of most species; even with respect to vertebrates other than birds concepts are deficient in descriptions of main characteristics and variations of territorial behavior. He suggests that it be viewed as a complex behavioral system based on a plurality of subsystems and expressed in a spatial-temporal frame of reference. If territoriality is a behavioral system of broad spectrum, then several corollaries appear to follow: (1) study of its expression will not be easy; (2) constancy of its expression from group to group or in individuals of a given group can not be anticipated; (3) uniqueness of biological significance or function may not be served.

The classical concepts and historical development of territoriality have been summarized in the well-known papers by Nice (1933, 1941). Based on bird behavior, the central reactions or requisite behavior according to Nice (1941) appear to be the following: (1) spacing of pairs through pugnacity of males towards others of their own species and sex; (2) use of signals to warn away other males and to attract females; (3) fighting of males primarily for territory and not for mates; and (4) superiority and/or near invincibility of a male within his own territory. Discussion of the validity of these conditions for territoriality for all animals is beyond the scope of this paper. More information obtains on the spacing and signalling components in Odonata; however, Jacobs (1955) has shown that a territorial male dragonfly shows superiority in a number of ways. Superiority, however, seems to be more a concomitant than condition of territorial behavior since it appears to be a result of greater familiarity of the occupant with his peculiar area.

Although the literature on Odonata contains frequent references to spacing, localization and territorial behavior, the

systematic and critical investigation of one or more of these phenomena has been limited to the studies by Borror (1934), St. Quentin (1934), Moore (1952), Jacobs (1955), and Kormondy (1959). The latter four of these papers serve as the basis for determining the expression of territoriality in Odonata.

With respect to spacing, Moore (1953) found that the length of beat of solitary male dragonflies varies from more than 8 and up to 170 yards. When more individuals were present, the minimum spacing was 13 dragonflies per 100 yards (8 yards per dragonfly), irrespective of the number of species present. At peak population density in *Tetragoneuria* the minimum spacing was 3 to 10 yards, whereas when only solitary individuals were flying, the length of beat was as much as 50 to 100 yards. Dependence of the degree of spacing on population density has been recognized in other studies. That spacing behavior is an aspect of and is regulated by reproductive behavior is proposed by Moore and supported by my studies on *Tetragoneuria*. Spacing has no obligate relationship to localization, i.e., the constancy of association of a given male with a given area. Borror, for example, found a high degree of localization but no spacing to be characteristic of *Argia moesta*, *Hetaerina americana* and *Argia sedula*; Moore reported spacing but very little or no localization in the several species he studied. On the other hand, Jacobs reported that *Plathemis lydia* showed spacing and definite localization to specific sectors of the study area; many individuals returned to sectors previously occupied after having been absent for as long as five days. Apparent localization in *Tetragoneuria* can as well be interpreted as being fortuitous since the data are so meagre. Concern with the duration of localization as a prerequisite for postulating territoriality however, seems to be of less value than deciphering interactional behavior of males in localized areas.

With respect to interactions occurring intra- and inter-specifically in spaced dragonflies, behavior in no small measure appears to be modulated by the discriminatory ability of the occupant dragonfly. Using tethered individuals of seven species Moore showed that there is a greater ability to distinguish kind than sex in species which are not strongly dimorphic. The vast majority of potential interspecific miscegenations never passed

what Moore termed the "approach" stage, whereas intraspecific male clashes were rather the rule. It appears from his data that the highest frequency of intraspecific clashes occurred where significant morphological differences between the sexes are lacking. Erroneous attacks of either an inter- or intraspecific nature may occur in animals in a heightened state, according to Tinbergen (1953), if the foreign species or other male presents a stimulus which normally triggers the attack reaction.

With regard to signalling as a means of deterring other males and/or attracting females, the data are such that we cannot determine the innate and learned components and reactions. Jacobs has shown that in *Plathemis lydia*, a sexually dimorphic species, signalling among males is by dashes at one another, pursuit displays and dual flights, whereas in *Perithemis tenera*, also a sexually dimorphic species, it is effected by wing fluttering and pursuit flights. In the non-sexually dimorphic *Tetragoneuria*, males appear to learn to avoid occupied areas the signal being the mere presence of the occupant male. Moore concluded that individuals learn to avoid sites of previous encounters with rival males which they cannot distinguish from females. In any event, whether the signal is by chase, challenge, display, or mere presence, innate or learned, elimination of males from the immediate occupied area occurs.

Three major functions of territoriality in Odonata have been proposed: (1) to provide the male with a hunting (i.e., feeding) ground; (2) to serve in sexual selection and isolation; (3) to aid in dispersal. The first point was advanced by St. Quentin in his concept of the "Jagdrevier"; however, available evidence indicates that the primary reason for many or most dragonflies being at the water is mating. It is true that crepuscular aeshnines and certain cordulines feed over water on swarming mayflies; however, the characteristics of this feeding flight are quite different from those involved during reproductive flight. Regarding the second function, Williamson (1906) postulated, without critical evidence, that intraspecific male conflict may lead to sexual isolation, a point verified by my work in *Tetragoneuria*; Jacobs has shown experimentally the role of territory in sexual selection in *Plathemis lydia* and *Perithemis tenera*.

DISPERSAL

Moore proposed that spacing of individuals, which is dispersal in the breeding area, leads to dispersal of some individuals away from the breeding area. This point is probably the most difficult to establish experimentally or observationally. Marking-recapture or marking-sighting studies, of admitted limited application and success, appear to be the only practical methods available at the moment. In consequence, this section is more speculative, consisting largely of hypotheses hopefully provoking criticism and future study.

It was stated above that the amount of spacing varies directly with population density but has a minimum range; when this minimum is approximated or reached the area is, as it were, saturated. At this point incoming males cannot be accommodated but must leave the area. It is not known if they disperse in a density related fashion as proposed by Bovbjerg (1959) for animals demonstrating intraspecific aggressive behavior.

Possible attributes of dispersal as a function of territoriality may be considered in several major categories: (1) preventing or lessening interference of a male with an ovipositing female; (2) avoiding overcrowding of a restricted breeding area; (3) populating newly opened or reopened areas. If species copulate away from the water, as do those which Moore studied, limited spatial dispersal is not the means of preventing interference in copulation, but the flight away is. Jacobs argues that since territorial behavior reduces the potential number of males at the breeding area, potential interference with oviposition is thereby removed. Jacobs also shows that in situations in which the male holds the female during oviposition, as in *Enallagma aspersum*, there is no territorial behavior.

In preventing overcrowding of the restricted breeding area, dispersal may affect the adult by preventing a further increase in adults before density-dependent mortality factors could act on population size. By promoting more uniform occupancy of local fragments of the environment there is an increased likelihood that a courting female would be mated with. If the territory includes the oviposition site, as in *Plathemis* and *Perithemis*, one concomitant might be a lessening of potential larval density;

if the oviposition site is outside the mating territory, as in *Tetragoneuria*, this function could hardly be served. In fact, any benefit of spacing in potentially preventing overcrowding of larvae is controverted by aggregational oviposition behavior in *Tetragoneuria*. Possibly the major factor resulting from territorial induced dispersal occurs through the exclusion of some males from the breeding area inasmuch as this not only samples the gene pool but does so in a small interbreeding population.

Dispersal in the broader sense is the means of populating newly available or reopened areas, but the role of territoriality in this phenomenon is essentially unstudied. A major deficiency in evidence of such factors as incidence, rates, and directions of Odonata population movements is also acknowledged. Wolfenberger (1946) shows that as one proceeds out of a center of dispersion not only does the number of insects drop off rapidly, but those which continue to disperse do so at a less rapid rate of movement. His evidence also indicates that dispersion occurs over greater distances where populations at the origin are denser. Although there is no evidence available in Odonata to apply directly here, it is noted that spacing behavior is largely known to occur in libellulines, the group to which belong most migrant species.

The common assumption that Odonata are readily dispersed appears to be based in no small measure on the strong flight powers of many of its members, and/or on the light-bodied damselflies which should be easily dispersed by wind, updrafts, and currents. That they are not so readily dispersed appears to be borne out by several lines of work, the former by records of migratory and/or swarming species and the localization studies discussed above, and the latter by studies on the distribution of Odonata in and by the air. Regarding the latter point Glick (1939) reported twenty-one Odonata taken at altitudes of 20 to 3000 feet (only one Zygoptera at the latter height), with only seven species (four Anisoptera, three Zygoptera) represented. No strong fliers were taken over 1000 feet although some were observed as high as 7000 feet. On the other hand, the widely distributed *Anomalagrion hastatum* (Say), one of the smallest and weakest Zygoptera, was relatively the most abundant form in the upper air. Although it would seem reasonable that light-

bodied forms might be updrafted and dispersed by wind action, very few were; it seems equally unlikely that strong fliers would be so affected. Glick's totals are, unfortunately, too small to serve as any more than speculative spring-boards. Felt (1928), in summarizing dispersal of insects by air currents, concluded that dispersal of such large forms as species of *Anax*, *Aeshna* and *Tamea* is due more to their inherent ability to remain in the air for considerable periods than as a result of wind currents.

Although migratory species have been reported among calopterygines, agrionines, aeshnines and libellulines, it cannot be said that migratory behavior is widespread in Odonata. Of some 5000 known species, probably less than 25 to 50 are known to be migratory. Williams (1958), mentions 13 migrant species of Odonata. The British Isles, for example, have been invaded on numerous occasions but the species involved have been few. One of the most extensive recent migrations occurred in 1947 and involved *Sympetrum striolatum nigrifemur* apparently from the coast of Spain and Portugal (Longfield, 1948).

In North America, the reported migrants seem to be: *Aeshna clepsydra*, attributed by Brown to have annual migrations in Wisconsin (Calvert, 1893); *Anax junius*, *Libellula pulchella* and *Tamea lacerata* which, according to Shannon (1916), follow regular annual migration routes along the Atlantic Coast similar to those of birds and involving as many as 360,000 individuals (in this connection, *Anax junius* and *Tamea lacerata* were reported by Borror (1953) as constituting 90% of a migratory flight on Long Island); *Pantala flavescens* and *Tamea carolina*, which along with *Anax junius* have a definite migration for the purpose of obtaining food (Wright, 1945). Walker (1953), however, states: "We know of no reports of dragonfly migrations in Canada, although the occurrence of swarms of certain species is no rarity." I have elsewhere (1959) reported on four swarms of 50 to 100 individuals involving the three northern species of *Tetragoneuria* with six other species. Whether swarming is related to migratory behavior is unknown; the most noted migrant, *Libellula quadrimaculata*, however, is widely distributed and is frequently observed in swarms. In sum, migratory behavior is an activity pattern limited to few species. Although it may be a mechanism of dispersal for these forms, regularly for some

and occasionally for others, migration does not seem to be the mode of dispersal for many. Further, what relationship obtains between migratory and territorial behavior is yet to be determined.

The preceding discussion has centered largely on the general nature of territoriality in Odonata with rather less detail on the role of this behavior in dispersal. This has been occasioned by the lack of systematic and quantitative data on dispersal, or on dispersal as an effect of territoriality. Considerably more needs to be learned of the range of expression of territorial behavior in Odonata, as well as in other invertebrates, and certainly much more needs to be learned of dispersal incidence, rates, direction, and associated factors. We are, it seems, still largely in the stage of knowing that certain dragonflies occur here and there, but have no valid data to indicate how they got from here to there. Two things we do seem to know: (1) that as far as the individual is concerned the tendency to react to a particular set of landmarks is a deterrent to dispersal, (2) that as far as the population is concerned, territoriality deters some individuals from moving and necessitates the movement of others.

SUMMARY

1. Territorial behavior in Odonata is reviewed with emphasis on spacing and signalling.
2. In Odonata (and other organisms), territoriality may function in sexual selection and in aiding dispersal. Dispersal is presumably significant in avoiding overcrowding effects in a restricted breeding area, lessening interference with oviposition, and populating newly opened or reopened areas.
3. The possibility of relationship between migration and/or swarming and territoriality is considered.

References Cited

- Borror, D. J. 1934. Ecological studies of *Argia moesta* Hagen (Odonata: Coenagrionidae) by means of marking. *Ohio Jour. Sci.* 34: 97-108.
- . 1953. A migratory flight of dragonflies. *Ent. News* 64: 204-205.
- Bovbjerg, R. V. 1959. Density and dispersal in laboratory crayfish populations. *Ecology* 40: 504-06.

- Calvert, P. P. 1893. Catalogue of the Odonata of the vicinity of Philadelphia. Trans. Amer. Ent. Soc. **22**: 152a-272.
- Carthy, J. D. 1958. An introduction to the behavior of invertebrates. Macmillan Co., New York.
- Carpenter, C. R. 1958. Territoriality: a review of concepts and problems. In: Behavior and Evolution, A. Roe and G. G. Simpson, Ed. Yale University Press.
- Crane, J. 1941. Crabs of the genus *Uca* from the west coast of Central America. Zoologica **26**: 145-208.
- Elton, C. 1932. Territory among wood ants (*Formica rufa* L.) at Pickett Hill. Jour. Anim. Ecol. **1**: 69-76.
- Felt, E. P. 1928. Dispersal of insects by air currents. New York State Mus. Bull. **274**: 59-129.
- Glick, P. A. 1939. The Distribution of Insects, Spiders, and Mites in the Air. U. S. D. A. Techn. Bull. **673**: 150 pp.
- Heape, W. 1931. Emigration, Immigration and Nomadism. Heffner, Cambridge.
- Howard, H. E. 1920. Territory in Bird Life. Murray, London.
- Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology **36**: 566-86.
- Kormondy, E. J. 1959. The systematics of *Tetragoneuria*, based on ecological, life history, and morphological evidence (Odonata: Corduliidae). Misc. Pub. Mus. Zool. Univ. Mich. **107**: 1-79.
- Longfield, C. 1948. A vast immigration of dragonflies into the south coast of Co. Cork. The Irish Naturalists' Jour. **9**: 133-41.
- Moore, N. W. 1952. On the so-called "territories" of dragonflies (Odonata-Anisoptera). Behavior **4**: 85-100.
- . 1953. Population density in adult dragonflies (Odonata-Anisoptera). Jour. Anim. Ecol. **22**: 344-59.
- Nice, M. M. 1933. The theory of territorialism and its development. In: 50 Years' Progress of American Ornithology. Lancaster, Amer. Ornith. Union: 89-100.
- . 1941. The role of territory in bird life. Amer. Midl. Nat. **26**: 441-87.
- Noble, G. K. 1939. The role of dominance in the life of birds. Auk **56**: 263-73.
- Pickles, W. 1935. Populations, territory and interrelations of the ants *Formica fusca*, *Acanthomyops niger*, and *Myrmica scabrinodis* at Garforth (Yorkshire). Jour. Anim. Ecol. **4**: 22-31.
- Pukowski, E. N. 1933. Oekologische Untersuchungen an *Necrophorus*. Zeits. Morph. ök. Tiere **27**: 518-86.
- Saint-Quentin, D. 1934. Beobachtungen und Versuche in Libellen in ihren Jagdrevieren. Konowia **13**: 275-82.
- Shannon, H. J. 1916. Insect migration as related to those of birds. Sci. Monthly **3**: 227-40.
- Thorpe, W. H. 1956. Learning and Instinct in Animals. Harvard Univ. Press.

- Tinbergen, N. 1953. *Social Behavior in Animals*. Methuen and Co., London.
- Verwey, J. 1930. Einiges über die Biologie Ost-Indischer Mangrokraben. *Treubia* 12: 167-261.
- Walker, E. M. 1953. *The Odonata of Canada and Alaska, Vol. I*. Univ. Toronto Press.
- Williams, C. B. 1958. *Insect Migration*. Macmillan Co., New York.
- Williamson, E. B. 1906. The copulation of Odonata. *Ent. News* 17: 143.
- Wolfenberger, D. O. 1946. Dispersion of small organisms. *Amer. Midl. Nat.* 35: 1-152.
- Wright, M. 1945. Dragonflies predaceous on the stablefly *Stomoxys calcitrans* (L.). *Fla. Ent.* 28: 11-13.